CHARACTERISTICS OF KNEE JOINT RECEPTORS IN THE CAT

By P. R. BURGESS and F. J. CLARK

*From the Department of Physiology, University of Utah
College of Medicine, Salt Lake City, Utah, 84112, U.S.A. and
the School of Electrical Engineering and Department of
Veterinary Anatomy, Purdue University, W. Lafayette,
Indiana, 47907, U.S.A.*

SUMMARY

1. The conduction velocities of 278 posterior articular nerve fibres studied in dorsal root filaments ranged from 10 to 110 m/sec. The conduction velocities were distributed similarly to posterior articular nerve fibre diameters determined histologically.

2. Two hundred and nine fibres were slowly adapting. Of these, 140 responded only at both marked flexion and marked extension, forty-seven responded only during flexion and twelve only during extension. Four slowly adapting fibres were activated specifically at intermediate joint positions. Outward twist of the tibia (abducting the foot) enhanced the discharge of most slowly adapting joint fibres.

3. Two rapidly adapting receptor types were noted. Pacinian corpuscle-like receptors (fourteen fibres) responded transiently to joint movement in any direction regardless of initial position. Phasic joint receptors (thirty fibres) were rapidly adapting at most joint positions but could give a low rate sustained discharge when strongly stimulated.

4. Six slowly adapting posterior articular nerve fibres responded to succinylcholine, suggesting that they originated from muscle spindles. Spindle-like receptors were usually tonically active at intermediate joint positions.

5. Eleven slowly conducting myelinated fibres responded only to extreme joint movement, which was probably noxious.

INTRODUCTION

Activity reaching the central nervous system from peripheral receptors contains the information subsequently utilized for sensory discrimination, and the nature of this activity is presumably relevant to the functions it

serves. There is good evidence that sensory structures located within and around joints contribute to position sense (Stopford, 1921; Browne, Lee & Ring, 1954; Cohen, 1958; Provins, 1958; Gelfan & Carter, 1967). An understanding of the properties of joint receptors is therefore pertinent to an analysis of the neural mechanisms underlying an animal's ability to determine the relative position of its body parts. In the past, the characteristics of joint receptors have been studied utilizing gross recordings from entire articular nerves (Andrew & Dodt, 1953; Cohen, 1955; Skoglund, 1956) or by recording from single active fibres in strands dissected from such nerves (Andrew & Dodt, 1953; Boyd & Roberts, 1953; Cohen, 1955; Skoglund, 1956). The experiments using gross recording techniques have indicated that the greatest number of afferent impulses occur at or near the extremes of flexion and extension, with comparatively little activity in between. However, single fibre studies have dealt largely with receptors responding at intermediate positions and have not reflected a preponderance of activity at marked extension or flexion. In some cases, this bias apparently has resulted from the technique employed to study single fibres (recording from strands dissected from articular nerves); moving the joint to a position near maximum flexion or extension resulted in sufficiently increased activity in the strand that the discharges from particular receptors could no longer be reliably distinguished. In the experiments of Boyd & Roberts (1953), selection was imposed by the fact that the knee could not be flexed or extended much beyond the mid position because of the experimental arrangement. Since receptor properties can be accurately studied only by single unit recording, the characteristics of the majority of articular receptors have not been defined, and such fundamental questions as whether individual fibres respond both at extension and flexion have not been answered.

We have sought an experimental approach for isolating single joint fibres which would minimize and allow an estimation of any sampling bias. A suitable technique should indicate accurately the number of joint fibres being recorded from at any one time and should limit this number so that individual receptor activity can be easily recognized. In addition, the method should permit movement of the joint over its entire physiological range. These requirements seemed best satisfied by recording from dorsal-root filaments, each containing one or two fibres activated by electrical stimulation of the posterior articular nerve (the largest nerve innervating the cat knee joint (Gardner, 1944)). It has been possible to identify two previously undescribed receptor types with this technique, and to make an estimate of the frequency of occurrence of different receptors. Also, many slowly adapting receptors were revealed which responded both at flexion and extension.

METHODS

Adult cats were anaesthetized by intraperitoneal injection of sodium pentobarbitone (Nembutal, Abbott Laboratories, 35 mg/kg) and given supplemental doses as needed. In a few cases alpha-chloralose (Aero Chemical Co., 70 mg/kg) was used. Carotid arterial blood pressure was measured and, in most experiments, end-tidal CO_2 was monitored continuously. Rectal temperature was maintained at $37 \cdot 5 \pm 0 \cdot 2°$ C with external heat and a lamp was used to warm the hind limb.

The animals were rigidly mounted in a frame in the prone position. The hind limb was partially denervated by removing the biceps muscle and either cutting or crushing all branches of the sciatic nerve except the posterior articular nerve. The posterior articular nerve was partially freed from surrounding tissue and prepared for electrical stimulation.
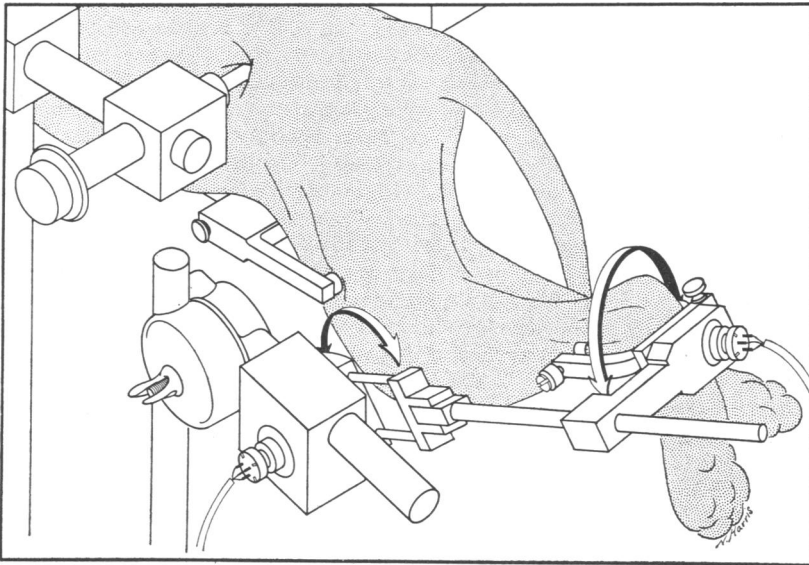

Fig. 1. Sketch of assembly used to measure knee joint angle and tibial twist. Slide bearings were used at knee pivot to accommodate slight misalignments and a shift in the centre of rotation as joint was moved. Joint position was monitored with potentiometers.

The femur was held with steel pins and a small device (Fig. 1) was attached to the tibia at a point near the foot, leaving the ankle joint free. This assembly permitted unimpeded movement of the leg throughout its physiological range (approximately 170°) and incorporated two potentiometers which measured the angle of the knee joint and the twist of the tibia.

A laminectomy was performed to expose the L 6–S 1 dorsal roots, and the skin was used to form a pool which was filled with warm mineral oil. The L 6 or L 7 dorsal root was divided under oil into naturally occurring fascicles and tested for active joint fibres by stimulating the posterior articular nerve. In some cases a pair of platinum wires was employed for stimulation, but when space was limited a single wire (cathode) was used, the anode being connected to surrounding tissue. No difference between the two methods of stimulation was observed. Typically, a rootlet contained several active posterior articular nerve fibres and it was repeatedly subdivided until filaments were obtained containing only one or two active fibres.

Peripheral conduction velocities were calculated from electrical response latencies measured at slightly suprathreshold and three times threshold stimulus strengths, and the conduction distance measured *in situ*. (A find thread was laid along the nerve bundle from the stimulating cathode to the recording point.) No allowance was made for utilization time at the stimulating electrode. Only slight shifts in latency (0·05–0·1 msec) were observed between just suprathreshold and thrice threshold shocks with the 100 μsec stimulus pulse duration used.

After several filaments had been prepared for recording, the stimulating electrode was removed from the posterior articular nerve. Each fibre was tested by moving the leg in a variety of ways, by tapping, and by pressing or probing about the knee. In later experiments a standardized procedure was also used in order to provide an accurate basis for comparing and classifying receptor responses. In this procedure the knee joint was held stationary at several positions to determine the adapted discharge rate versus angle characteristic. This test was performed with the tibia in the neutral (untwisted) position and also with the tibia maximally (but not forcibly) twisted in the 'outward' (foot abducted) and 'inward' (foot adducted) positions. The joint was then flexed and extended at angular rates of 60 and 150°/sec. To aid in producing accurate rates of flexion and extension an analog signal approximating the time derivative of the joint angle was displayed on an oscilloscope and also used to frequency-modulate an audio tone. The receptor discharge was presented on an oscilloscope as 'instantaneous' firing rate versus knee joint angle. The instantaneous firing rate was obtained using an electronic circuit which measured interspike intervals (expressed in seconds) and plotted their reciprocals. The oscilloscope display was scaled so that the ordinate showed an appropriate discharge rate and the abscissa represented the increasing angle between the tibia and femur as the joint was moved from the fully flexed position (10°) to complete extension (180°). The display was either photographed or sketched on pre-printed data sheets having the same format as the oscilloscope display.

In some experiments gross recordings of joint receptor activity were made from the posterior and medial articular nerves. The nerves were freed from surrounding tissue in the usual manner, cut and the peripheral portion placed on recording electrodes. The leg was not denervated. Single fibre activity could be easily distinguished because of the small size of the articular nerves. Signal-to-noise ratios were usually greater than 10 to 1 for fibres such as those of Pacinian corpuscle-like receptors which conducted at 60–70 m/sec (see below).

Most of the joint nerves were prepared for histological examination. Each nerve was washed in saline and fixed for 24–40 hr in either buffered (pH 7·4) 2 % osmium tetroxide or Flemming solution (1 % chromic acid, 15 ml.; 2 % osmic acid, 4 ml.; glacial acetic acid, 1 drop). The specimens were subsequently dehydrated, embedded in paraffin, and sectioned at 5 or 8 μ. The nerves fixed in the Flemming solution were later stained with a Weigert stain (Gutmann & Sanders, 1943).

RESULTS

Adequacy of the sample

It is important to know whether the population of fibres obtained by splitting dorsal-root filaments adequately represents the range of myelinated fibre sizes present in the posterior articular nerve. Figure 2*a* shows frequency of occurrence as a function of conduction velocity for the 278 posterior articular nerve fibres studied. Figure 2*b* illustrates the distribution of fibre diameters in ten nerves. No compensation was made for possible dimension changes during the histological procedures (Williams & Wendell-Smith, 1960). A comparison of Figs. 2*a* and *b* suggests that myeli-

nated axons of all sizes are represented in the sample of dorsal-root fibres, although there is some bias in favour of the larger fibres.

Receptor types

Receptors were first divided into two categories depending on whether they were slowly or rapidly adapting. Most slowly adapting receptors could be further divided into three types on the basis of their responses to joint movement. The rapidly adapting receptors were classed either as
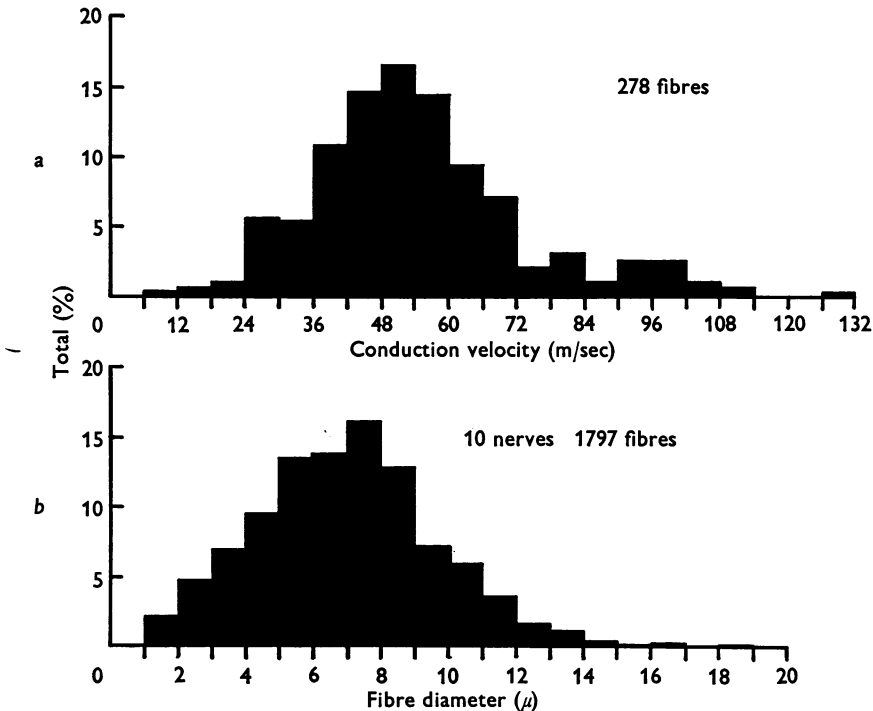

Fig. 2. Frequency of occurrence histograms of (a) conduction velocities of fibres studied in the dorsal roots and (b) fibre diameters in the histological sample. Posterior articular nerve.

Pacinian corpuscle-like or phasic joint receptors. Twenty-one receptors (7·6 %) were included in various minor categories and fourteen fibres (5·0 %) could not be activated by any form of stimulation used. These results are summarized in Table 1.

In the discussion which follows, the properties of the major slowly adapting receptor types will be considered first. To aid in the description of slowly adapting receptor characteristics, we have used the following terms: ACTIVATION ANGLE is defined as the number of degrees (measured between the tibia and femur) over which a prolonged discharge showing

TABLE 1. Summary of receptor types

Cat posterior articular nerve (278 fibres)

Receptor type	Number observed	Conduction velocity m/sec (95% or more fall into range shown)	Adaptation rate	Type of response
Flexion–extension	140 (50·4%)	30–70	Slow	Discharge only at or near the extremes of flexion and extension
Flexion	47 (16·9%)	20–70, 80–110	Slow	Discharge only at flexion with tibia not twisted, but 60% respond at most joint angles with outward tibial twist (see text)
Extension	12 (4·3%)	38–65	Slow	Discharge only at or near full extension
Phasic joint	30 (10·8%)	50–100	Intermediate	Predominantly phasic but capable of low rate sustained discharge. Respond to movement over part or all of range
Corpuscle-like	14 (5·0%)	55–83	Rapid	Respond with variable sensitivity only during joint movement
Other receptors	4 (1·4%)	—	Slow	Some response at intermediate joint angles (see text)
	11 (4·0%)	12–33	Variable	Possible nociceptors. Respond only to bending and twisting procedures considered noxious
	6 (2·2%)	34–107	Slow	Muscle spindle-like. Discharge increases in response to succinylcholine (0·1–0·2 mg i.v.)
	14 (5·0%)	5–125	—	Not activated. Six had conduction velocities < 30 m/sec

little or no adaptation can be produced with the leg systematically held stationary at various positions. In contrast, RESPONSE ANGLE is defined as the number of degrees over which activity can be obtained when the joint is moving. With extremely slow movement of the joint, activation and response angles approached congruence. Otherwise, the response angle exceeded the activation angle to varying degrees because the receptors were sensitive to the rate of joint movement. Some receptors had continuous activation and response angles. Others responded at near maxima of both flexion and extension, but not at intermediate positions. In the latter case we have considered the receptor to have two activation angles, one at flexion and the other at extension.

Flexion–extension receptors. Flexion–extension receptors constituted the largest group in the posterior articular nerve with 140 fibres or 50·4 % of the total. They were slowly adapting and responded only near the extremes of flexion and extension. Activation angles at either extreme, with the tibia untwisted, rarely exceeded 15°. Figure 3*a* shows the 'instantaneous' discharge rate (see Methods) of a flexion–extension receptor as a function of the angle between the femur and the tibia, with the tibia untwisted. The discharge rate is shown on the ordinate and the abscissa represents the increasing angle between the tibia and femur as the joint was moved from full flexion (10°) to complete extension (180°). Twisting the tibia 'outward' (abducting the foot) invariably increased the discharge rate and the activation angle (Fig. 3*b*), and the effect was greatest near maximum extension. Twisting the tibia 'inward' (adducting the foot) had variable effects. Seventy-five per cent of the flexion–extension receptors showed a decrease in activation angle and/or a reduction in the discharge rate at both flexion and extension. For the remaining receptors the discharge could be enhanced at either flexion or extension or both. Figure 3*c* illustrates a case where an inward twist of 30° enhanced the extension response but abolished the response in flexion.

The responses of flexion–extension receptors at flexion and extension were similar in 25 % of the cases. That is, the activation angles and maximum discharge rates were equivalent. The remaining fibres were approximately equally divided between those responding more vigorously at extension and those showing a greater response at flexion. The rare receptor which responded phasically at one extreme joint position and tonically at the other was also classified as a flexion–extension type.

The discharge of flexion–extension receptors was regular and could be maintained indefinitely, though sustained activity did not occur at rates less than 10–15 impulses/sec. The maximum steady-state response was not observed to exceed 150 impulses/sec, but transient responses in excess of 250/sec were seen with rapid changes in joint angle. With an abrupt change

in angle, there was a correspondingly abrupt change in the frequency followed by a several second period of adaptation to the characteristic steady-state level. The nature of the phasic response depended on the direction of movement. Moving further into the activation angle caused a temporary enhancement of the discharge while moving the opposite
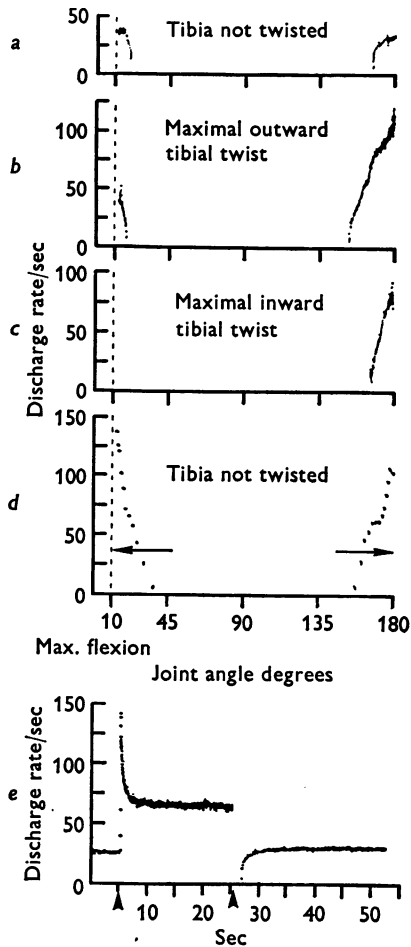

Fig. 3. Flexion-extension receptor response characteristics. 'Instantaneous' discharge rate calculated from time intervals between pairs of impulses and marked by a dot placed along the horizontal axis at the angle, (*a*), (*b*), (*c*) and (*d*), or time (*e*) of occurrence. The angle between the tibia and femur was 10° at maximum flexion, 180° at maximum extension. Steady-state response versus joint angle for tibia: (*a*) not twisted, (*b*) maximum outward twist, (*c*) maximum inward twist. (*d*) joint rotated at 150°/sec with arrows indicating direction of movement (tibia not twisted). (*e*) shows adaptation rate. Extension abruptly increased (1st arrow), held, and released (2nd arrow), with joint positioned near maximum extension and tibia twisted outward.

direction caused a temporary decrease in activity. In Fig. 3e, which shows instantaneous rate of discharge as a function of time, extension was abruptly increased at the first arrow, moving the joint further into the activation angle, and the leg was returned to its original position at the second arrow. With the knee joint angle fixed at an appropriate position, the response to tibial twist showed a similar directional dependence. This property will be referred to as bi-directional rate sensitivity.

The receptors were routinely tested at rotation rates of 60 and 150°/sec with the tibia untwisted. Response angles and discharge frequencies at these rotation rates were compared with the activation angles and steady-state frequencies of discharge previously determined with the leg held stationary at various positions. For 80 % of the receptors, the response angle exceeded the activation angle and the discharge frequency increased transiently above the steady-state level by equivalent amounts. The increases in frequency and angle varied from 20 to 200 %. A comparison of Figs. 3a and d shows this type of increase, the arrows in Fig. 3d indicating the direction of movement. Approximately 15 % of the receptors showed an increase in receptor discharge with the faster rates of joint rotation but response and activation angles differed little. In 5 % of the cases, response angles exceeded activation angles but there was little change in maximum discharge rate. An individual receptor could follow one pattern in flexion and another in extension.

All flexion–extension receptors responded with a lowly adapting discharge to pressure on the back of the knee. When 0·1–0·2 mg succinyl-choline chloride (Sucostrin, E. R. Squibb and Sons) was injected i.v. there was no significant change in the discharge rate.

Flexion–extension fibres had a wide range of conduction velocities; 95 % fell between 30 and 70 m/sec (Fig. 4a).

Flexion receptors. Flexion receptors were the second most common type encountered in these experiments, and forty-seven such receptors (16·9 % of the total) were studied. All flexion receptors were slowly adapting and the responses of 40 % were indistinguishable from the flexion responses of flexion–extension receptors. The remaining 60 % responded to joint rotation in a different manner. With the tibia untwisted, the activation angle could be as large as 60° (Fig. 5a). Typical bi-directional sensitivity to changing joint angle was present in flexion, and there was no response at extension. Inward twisting of the foot reduced the activation angle. In contrast, twisting the tibia outward 10–15° enhanced the response in flexion and caused some response to appear near extension (between 90 and 180°). With maximal outward twisting, the flexion and intermediate angle responses increased and the receptor responded over nearly the entire flexion–extension range (Fig. 5b). Figure 5c illustrates the maximal out-

ward tibial twist occurring as the knee was moved from flexion to extension. Thus with outward twist, flexion receptors often had a tonic discharge at or near maximum extension. However, this discharge always decreased as extreme extension was approached. Flexion receptors did not respond to succinylcholine chloride (0·1–0·2 mg I.V.).
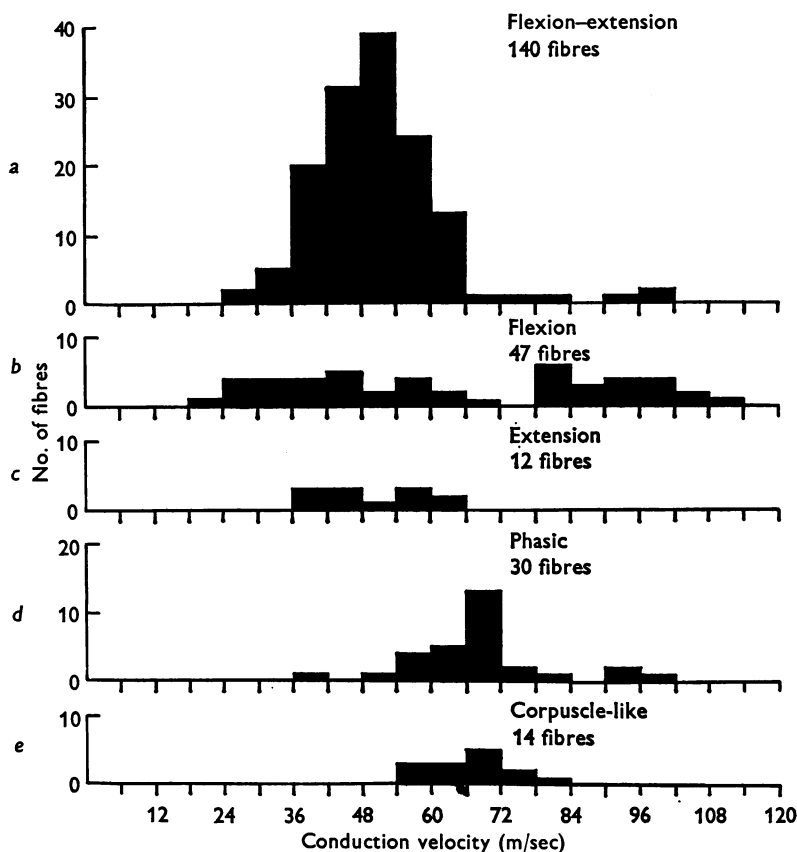

Fig. 4. Frequency of occurrence versus fibre conduction velocity for the various receptor types studied. Posterior articular nerve.

The conduction velocity histogram for flexion fibres (Fig. 4*b*) shows a broad distribution between 20 and 70 m/sec, and a second grouping between 80 and 110 m/sec. Forty-two per cent of the fibres were in the faster group. There was no correlation in our analysis between the conduction velocity of a flexion fibre and its response to flexion, extension or twist of the tibia.

Extension receptors. Twelve fibres (4·3 %) were of the extension type. Except for the absence of any response in flexion, the characteristics of

these receptors were the same as flexion–extension receptors. Extension fibres had conduction velocities between 38 and 65 m/sec (Fig. 4c).

Phasic joint receptors. Thirty receptors (10·8 % of the total) were found which responded primarily to joint movement, but were also capable of a low rate (less than 10/sec) sustained discharge (Fig. 6). With the tibia untwisted, joint movement produced a transient response at the extremes of flexion and extension which was bi-directionally sensitive. However,
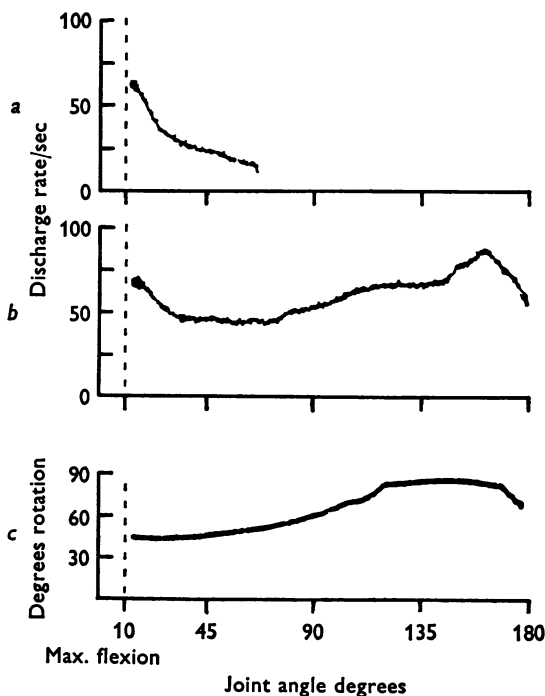

Fig. 5. Characteristics of the flexion receptor type showing steady-state discharge over entire flexion–extension range with outward tibial twist. Some 60 % of the flexion type behaved in this manner (see text). (a) shows response with tibia not twisted, (b) response with maximal outward twist. Maximal outward tibial twist varied with joint angle as shown in (c).

with an outward twist of the tibia, almost all of these receptors responded transiently to joint movement in either direction throughout the physiological range. In about 25 % of the cases, a low-level sustained discharge could be produced by the combination of strong outward twist and maximum extension and in two cases outward tibial twist produced a sustained discharge at all joint angles. For all but three of the receptors, it was possible to locate a focus of sensitivity on the lateral (thirteen fibres), the medial (twelve fibres) or the patellar (two fibres) aspects of the knee. Gently pressing on the area with a glass rod or the fingers was a potent

stimulus, and it was possible to demonstrate the low rate sustained component of the discharge by steady pressure on the focus even when tonic activity could not be produced by joint rotation.

Most phasic type fibres conducted between 55 and 75 m/sec (Fig. 4d). Phasic joint receptors did not respond to succinylcholine chloride (0·1–0·2 mg i.v.).

Pacinian corpuscle-like receptors. Fourteen receptors (5·0 %) were studied whose discharge was characteristic of that described for Pacinian corpuscles
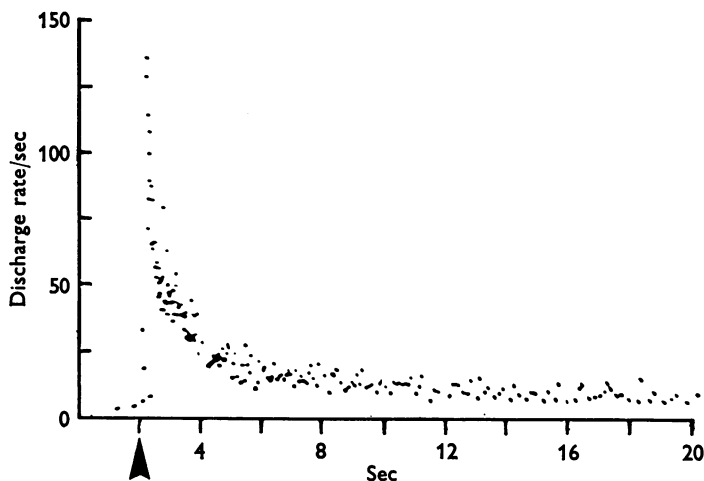

Fig. 6. Discharge characteristics of phasic joint receptor. Small increment of outward tibial twist abruptly applied (at arrow) and maintained. The discharge continued for many seconds and only the initial part is shown. Joint positioned near maximum extension.

(Gray & Matthews, 1951; Hunt, 1961). They could be activated easily by tapping the leg with a glass rod, and sometimes fired in synchrony with the arterial pulse. Corpuscle-like receptors could be excited by rapid joint movement in any direction regardless of position. The response was invariably rapidly adapting, activity occurring only during joint movement. Corpuscle-like receptors were supplied by fibres conducting between 55 and 83 m/sec (Fig. 4e).

Other receptor types. Twenty-one fibres responding to joint rotation (7·6 %) could not be classified into any one of the preceding groups. Of these, six bore some resemblance to muscle spindle afferents. They were slowly adapting and responded to joint movement, but in contrast to typical joint receptors all responded to succinylcholine chloride (0·1–0·2 mg i.v.). This drug excites muscle spindle afferent fibres (Smith, 1963). To test the possibility that spindle-like afferents might regularly be found in the posterior articular nerve, gross recordings were made from the nerve

before and after administration of succinylcholine. Figure 7*a* shows the discharge present at a joint angle of 100° before succinylcholine and Fig. 7*b* the increased activity occurring after 0·1 mg of the drug was administered I.V. These results were typical and indicate a contribution from spindle-like receptors. Pressing about the capsule and sides of the knee did not alter the discharge of these receptors except in two instances where
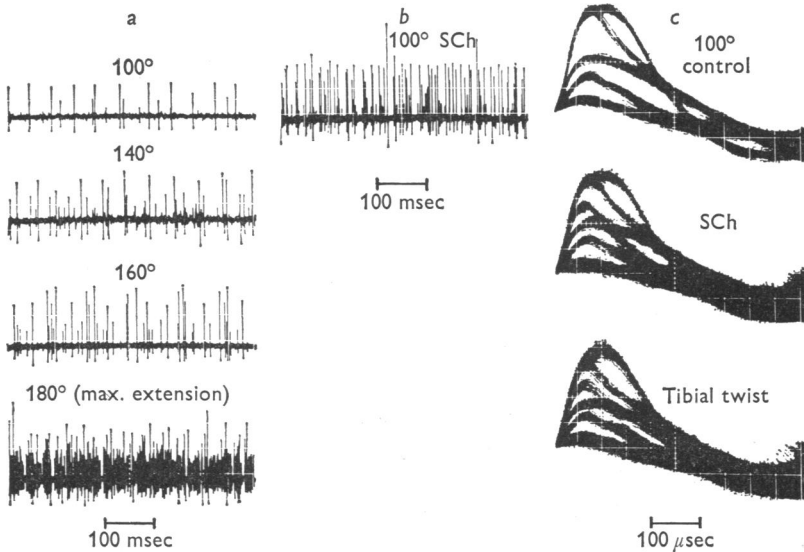

Fig. 7. Gross recordings from the entire posterior articular nerve (*a*) at various intermediate angles and at maximum extension. (*b*) is the effect of succinylcholine chloride, SCh (0·1 mg I.V.) at joint angle of 100°. (*c*) shows records obtained from the posterior nerve by superimposing all the impulses occurring during a 2–4 sec period. Five potentials are apparent in the first record. Both SCh and tibial twist activated only one additional fibre. Twisting the tibia usually altered the wave forms slightly, probably due to small shifts in the position of the nerve on the recording electrodes.

activation was obtained from a poorly defined location outside the joint. Since the location and morphology of these receptors is not known, their identification as muscle spindles remains uncertain.

Two fibres (27 and 57 m/sec) had intermediate activation angles, and two more (47 and 54 m/sec) responded phasically at intermediate positions. The 27 m/sec fibre responded over the entire range of joint angles when the tibia was strongly twisted outwards, with a peak at 20–30° from maximum extension. There was no response with the tibia in the neutral position. The 57 m/sec fibre had an activation angle of 30° situated near maximum flexion, and the response was broadly peaked within this range. Inward twist of the foot shifted the response curve some 30° away from maximum

flexion, but did not alter its shape. Outward twisting had no effect. The 47 m/sec fibre responded much like an extension type except for a phasic response over a narrow range (approximately 15°) slightly displaced from maximum flexion. The 54 m/sec fibre behaved as a flexion fibre when tested with the tibia not twisted. With outward twisting of the foot, the flexion response disappeared and the receptor responded at extension with a 40° activation angle. Rotation of the joint at 60 and 150°/sec along with outward tibial twist enhanced this extension response and also revealed a phasic response over a narrow range (15–20°) near maximum flexion.

Eleven fibres (4·0 %) responded only to bending or twisting procedures which could be considered noxious. The discharge produced by sustained stimulation was maintained at a low level (less than 15/sec) and persisted for 5–10 sec after termination of the stimulus. The conduction velocities of these fibres fell between 10 and 35 m/sec.

The remaining fourteen fibres (5·0 %) were not activated by moderate joint rotation, tapping or probing about the knee. Six of these fibres had conduction velocities under 30 m/sec.

Gross recordings from posterior and medial articular nerves

A series of experiments was performed to establish whether the pattern of activity recorded from the entire posterior articular nerve was consistent with the conclusion from single fibre studies that relatively few receptors responded tonically at intermediate joint angles. Figure 7 summarizes the results of a typical experiment.

At intermediate angles there was relatively little sustained activity (Fig. 7a). Activity increased slightly as the angle increased to 170–175°, whereupon the discharge became appreciable. The greatest activity occurred at maximum extension (180°). Maximum flexion could not be tested because of the location of the recording electrodes. At intermediate angles (e.g. 100°), the activity could be increased both by slight (5–10°) outward twist of the tibia or by succinylcholine (SCh) (0·1–0·2 mg I.V.), and it appeared that the same population of receptors was activated by both procedures. Figure 7c shows activity which has been recorded so that the wave forms of the impulses can be distinguished. A storage oscilloscope was used, and the triggering level set so that all the action potentials occurring in a several second period were superimposed. Potentials of different shapes originated from different fibres, and an indication of the number of active nerve fibres can be obtained by this method. The maintained discharge at a joint angle of 100° is illustrated, as well as activity evoked by SCh and outward tibial twist at the same joint angle. SCh and tibial twist, although greatly increasing the over-all activity, apparently activated only one fibre not present in the control record. Thus, in this

experiment, the activity at 100° appeared to be due largely to receptors which responded to SCh.

Gross recordings from the medial articular nerve showed marked activity at the extremes of flexion and extension. Figure 8 shows the response at maximum extension and at various intermediate positions. At intermediate angles there was relatively little discharge and positions were found with only one or two and sometimes no fibre active. Therefore, fibres in the medial and posterior articular nerves responded in a similar fashion over the flexion–extension range where comparisons were possible.
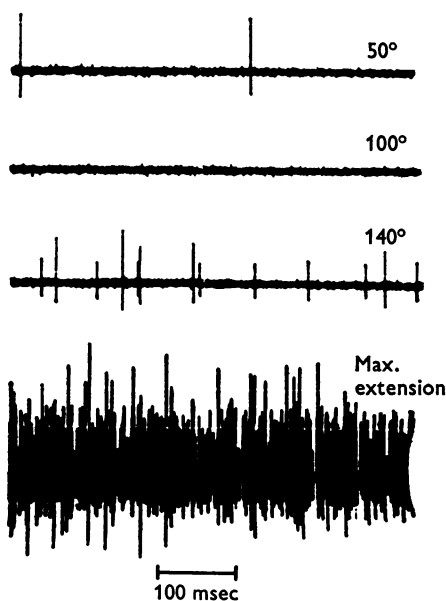

Fig. 8. Gross recordings from the medial articular nerve at various intermediate angles and at maximum extension.

DISCUSSION

One of the principal aims of the present experiments has been to study single joint fibres using a method that would allow an adequate description of the over-all pattern of activity reaching the spinal cord from the posterior articular nerve. The conduction velocity of each joint fibre was measured and the entire population of conduction velocities compared with fibre diameters in the posterior articular nerve. Conduction velocities ranged from 10–110 m/sec and were distributed in a fashion that generally paralleled the fibre diameter spectrum, although there was some bias in favour of the larger fibres. It seems reasonable to conclude, therefore, that the major receptor types present in the posterior articular nerve have been

observed in these experiments, and that the relative proportions of different fibres conducting at comparable velocities have been fairly sampled.

Consistent with the results of gross recording, most single fibres responded only during marked flexion or extension of the joint. Furthermore, 67 % of the slowly adapting receptors responded at both flexion and extension. Among previous investigators, Skoglund (1956) in particular has emphasized that impulse traffic over joint nerves increases greatly as maximum extension or flexion is approached and that relatively few receptors are active at intermediate positions. His single fibre studies included little description of the numerous receptors responding at marked flexion and extension, but fibres in the medial articular nerve which responded at intermediate positions and had relatively small activation angles were illustrated. We have observed a small number of joint receptors of this type in the posterior nerve, and would agree with Skoglund that although such receptors are present they are relatively uncommon. In the posterior nerve, most of the tonic activity present at intermediate joint angles, excluding that derived from spindle-like receptors, was contributed by receptors of the flexion type, and whether the discharge at intermediate positions was over a very small angle, over the entire flexion–extension range, or present at all depended on the degree of outward tibial twist.

The methods used in the present experiments have not only shown that most slowly adapting receptors respond both at flexion and extension, but also have revealed two previously undescribed receptor types: phasic joint receptors and high threshold receptors. Phasic joint receptors responded mainly to movement, but were also capable of some low level (less than 10/sec) sustained activity. They resemble in rate of adaptation some of the newly described field receptors in the hairy skin of the cat (Burgess, Petit & Warren, 1968). The knee joint, like the skin, possesses receptors with a range of adaptation rates. The high threshold joint receptors had slowly conducting myelinated fibres and probably function as nociceptors. They represent another example of high threshold receptors associated with small myelinated fibres; such receptors have now been found in joint tissues, muscle (Paintal, 1960; Bessou & Laporte, 1961) and skin (Burgess & Perl, 1967).

A few fibres in the posterior articular nerve resembled muscle spindle afferents. They alone among posterior articular nerve fibres responded to succinylcholine. In the experiment illustrated in Fig. 7, at least six spindle-like fibres were present and five responded at intermediate joint positions. Skoglund (1956) reported that the few fibres he found tonically active at intermediate angles in the posterior nerve could not be excited by manipulating the posterior capsule and suggested the cruciate ligaments as a possible location. We also were unable to excite receptors of this type by

pressing on the posterior capsule or other portions of the knee. Although such findings are consistent with the idea that these fibres originated from muscle spindles, positive identification cannot be made until the location and morphology of the receptors is known.

The experiments of Boyd & Roberts (1953) represent the only previous detailed single fibre study of the posterior articular nerve. The results obtained by these investigators are difficult to compare with our own because the recording method they used restricted joint movement to between 85 and 140°, and no attempt was made to sample adequately the population of joint fibres. In contrast to Skoglund (1956), they did not attempt to evaluate the nature of the bias in their single unit population by describing the pattern of activity obtainable by gross recording from the entire nerve. Boyd & Roberts noted that many receptors responded or showed enhanced discharge when the tibia was twisted outward and that inward rotation was far less effective, with which the present results agree. The large number of receptors they described responding only to outward twisting of the tibia would likely have responded at extreme flexion or extension or both if the joint could have been moved to these positions. A certain number of receptors were found which began to respond at inter-mediate positions when the leg was flexed, but did not show increased activity with outward tibial twist. Because joint movement was restricted, it could not be determined whether these receptors discharged at pro-gressively higher frequencies as the leg was moved to full flexion. Most of the flexion receptors we have observed discharging at intermediate posi-tions showed increased activation angles with outward tibial twist, and the responses observed by Boyd & Roberts may, therefore, represent the activity of receptors responding specifically at intermediate angles.

The flexion–extension, the extension and most flexion receptors could be easily excited by pressure on the back of the knee, suggesting that they lie in the capsule. Since the dominant receptor type in the capsule is the Ruffini ending (Gardner, 1944; Boyd, 1954; Skoglund, 1956; Freeman & Wyke, 1967), it is likely that Ruffini endings account for this type of response and are slowly adapting, as has been suggested by others (Boyd, 1954; Eklund & Skoglund, 1960). Some rapidly conducting fibres of the flexion type could not be activated by pressure on the back of the knee, but were excited by pressure on the sides of the joint. On the basis of location and conduction velocity, these fibres could be associated with the Golgi endings that have been described in the ligaments (Samuel, 1948; Andrew, 1954; Boyd, 1954; Skoglund, 1956; Freeman & Wyke, 1967), but further study will be required to establish this connexion.

Among the more rapidly adapting receptors, the Pacinian corpuscle-like receptors responded only to joint movement while phasic joint receptors,

though responding mainly to movement, were capable of some sustained activity. The presence of lamellated corpuscles in joint tissues (Samuel, 1948; Boyd, 1954; Skoglund, 1956; Hromada & Poláček, 1958; Freeman & Wyke, 1967) supports the correlation of the corpuscle-like receptor type with Paciniform endings. Phasic joint receptors were not excited by pressing the back of the knee, and although most were activated by pressure on the sides of the joint, the exact location of the receptors is not known.

The value of greatly enhanced articular nerve activity at the extremes of flexion and extension for the discrimination of knee joint position is not immediately obvious. The many slowly adapting fibres responding at both flexion and extension are particularly difficult to evaluate in this connexion. It may be that such fibres have little to do with position sense and function primarily in other systems. An examination of the central connexions of different types of joint fibres should be of value in determining their functional significance.

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